Differences in the ecology and distribution of lotic pulmonate and prosobranch gastropods

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Abstract: We hypothesize that pulmonate gastropods, in comparison to prosobranchs should (1) be better competitors because of finely-toothed radulae, (2) be better adapted to variable habitats because of greater powers of physiological regulation, (3) be better dispersers, but (4) face greater risk of predation. In the Salt River, in western Kentucky, U. S. A., pulmonates were fairly common in headwater streams, and were replaced in larger order tributaries by prosobranch snails. The literature suggests that pulmonates have tolerance and capacity adaptations to variation in physicochemical variables like temperature or dissolved oxygen. Only one of the two pulmonates tested in the laboratory, however, had quicker righting responses and rates of movement, important in recolonizing ephemeral habitats. A competition experiment in an artificial stream indicated that the large-river prosobranch, *Lithasia obovata* (Say, 1829), suffered less reduction in growth than the pulmonate *Helisoma trivolvis* (Say, 1817). Both the literature and experiments we have performed suggest that prosobranchs are less vulnerable to predators. We interpret these results to suggest pulmonates are more common in temporary headwater streams, or shallow littoral margins of lotic systems, because of greater physiological adaptation, while prosobranchs are more common in larger rivers (or in spring-fed rivers) because of greater competitive ability, lower risk of predation, or less-variable physicochemical regimes.

Key words: pulmonates, prosobranchs, distributions, competition, predation

The threat of extinction to freshwater unionid mussels from habitat alteration and the introduction of exotic species is well known, with almost one-third of the approximately 300 species in the United States either endangered or threatened (Neves *et al.*, 1998). In comparison, freshwater gastropods are even more diverse, with over 500 species recorded in the United States, and an especially high diversity in the southeastern states. Particularly at risk are the diverse Mobile and Tennessee River basin hydrobiids and pleurocerids, whose ecology and life histories are relatively unknown (Neves *et al.*, 1998). It is likely that this rich gastropod fauna is susceptible to some of the same threats as are unionids: impoundments, exotic species, channelization, and pollution (Jenkinson and Todd, 1998).

Although they have not received the attention that unionids have garnered, lotic gastropods can be important to ecosystem function. High densities of gastropod grazers can result in shifts in periphyton assemblages from long filamentous green algae, to more resistant forms such as adnate diatoms or toxic cyanobacteria (reviewed by Brown, 1991). For example, the pleurocerid *Elimia* can reduce periphyton biomass in southeastern rivers (see Rosemond *et al.*, 1993, and others reviewed therein). Because lotic gastropods are so diverse, are potentially at risk, and have important impacts on riverine ecosystems, more emphasis should be placed on understanding their ecology. The objective of this paper is to take a step in this direction by trying to understand ecological interactions between two prominent gastropod groups found in lotic systems, *i. e.* pulmonate and prosobranch snails.

Our approach is to review the ecology and basic biology of both groups, and formulate some hypotheses for why their habitat distributions differ. We argue that key factors explaining these distributional differences include relative dispersal abilities, competitive abilities, physiological adaptations to stressor variables, and predation risk.

Comparative ecology of pulmonates and prosobranchs

Pulmonates and prosobranchs differ in their evolutionary biology, ecology, and impact on lotic systems (Russell-Hunter, 1978; Brown, 1983, 1991; McMahon, 1983). Pulmonates have secondarily reinvaded freshwaters (from terrestrial intermediates) and range from amphibious to fully aquatic. Members of the families Lymnaeidae and Physidae rely on aerial respiration and are somewhat amphibious, whereas ancylids (limpets) and planorbids have secondarily-derived epithelial gills or dedicated respiratory pigments and are truly aquatic. The gilled prosobranchs evidently invaded lotic systems from estuaries

(McMahon, 1983) and many have longer life cycles, reduced reproductive effort, and greater iteroparity in comparison to most pulmonates (Browne, 1978; Browne and Russell-Hunter, 1978; Aldridge, 1983; Brown, 1983). Prosobranchs are often more streamlined (with the exception of the pulmonate ancylids) and therefore more resistant to being displaced by currents (Dussart, 1987). For example, pulmonate planospiral or globose shell shapes (*Helisoma* [= *Planorbella*] or *Physella* [= *Physa*], respectively) have higher drag coefficients. In fact, the only prosobranch family with globose shells, the viviparids, are characteristic of lentic or lotic habitats with little flow. Pulmonates, because of their "lungs," can passively disperse on birds (see references in Brown, 1991), and they therefore could have higher dispersal rates and lower levels of endemism (Davis, 1982).

Consequently, we could expect that pulmonates, with their higher reproductive rates, shorter life cycles, greater dispersal abilities (Davis, 1982; Brown, 1991), and air-breathing habits, should be superior at recolonizing temporary streams or headwater habitats previously denuded by spates or exposed by droughts. Although no one to our knowledge has directly tested the hypothesis of greater rates of passive dispersal in pulmonates, prosobranchs (with the possible exception of smaller species like hydrobiids) would seem to be restricted to adult dispersal along steam channels, perhaps explaining the greater degree of genetic isolation and endemism in prosobranchs (Davis, 1982).

Physiological factors can influence the distributions of species as well. For example, temporary streams or backwaters without much riparian cover often experience extreme temperatures because of their shallow depths and periodic droughts. Potentially lethal temperature stress, hypoxic conditions, or desiccation are likely in stagnant pools or exposed stream beds during drought conditions. As a result, increased resistance and capacity adaptations to temperature and dissolved oxygen variation should be selected for, as they are in other invertebrates or fish species that are characteristically found in temporary streams (Horwitz, 1978; Matthews, 1988; Moyle, 1988; Miller and Golladay, 1996; Jacobi and Cary, 1996; Williams, 1996). Alternately, if streams arise from springs, variation in physicochemical variables may increase away from spring sources, favoring more tolerant species downstream from springs.

In temporary headwaters, crayfish and other invertebrate predators probably achieve their greatest importance, as they do in temporary, fishless ponds (Lodge *et al.*, 1987). In more permanent lentic habitats, fish predators become a more significant factor (Brown and DeVries, 1985; Bronmark *et al.*, 1992), and similar trends occur in higher order lotic habitats as well (Horwitz, 1978). For example, in a Kentucky stream, fish diversity increased from one species in a headwater stream to 15 in a third-order river (Lotrich, 1973), and nearly 150 fish species exist in the Ohio River (Pearson and Krumholz, 1984). The fraction of predatory fish also increases with stream order (Moyle, 1988). Therefore, in headwaters or other temporary lotic habitats we predict that responses to low predation pressure should be only behavioral, for example, crawling out of the stream (Alexander and Covich, 1991a, b; Covich *et al.*, 1994). Morphological defenses (thick and sometimes knobby shells) would be expected to occur in large, unglaciated rivers, both because fish prefer thin-shelled species (Stein *et al.*, 1984) and because of the longer evolutionary time for selection of morphological defenses (Vermeij and Covich, 1978; Vermeij, 1987).

Considerable experimental evidence exists that predators can control the structure of lentic gastropod assemblages (Brown and DeVries, 1985; Sheldon, 1987; Kesler and Munns, 1989; Bronmark *et al.*, 1992; Lodge *et al.*, 1994). Comparatively little information about lotic assemblages is available, although predators clearly affect at least some gastropod populations in streams (Crowl, 1990; Crowl and Covich, 1990; Covich *et al.*, 1994).

In regard to relative competitive ability, some experimental evidence suggests pulmonates could be better competitors, at least in lentic systems, because they possess smaller, more numerous radular teeth and can efficiently remove adnate periphyton, whereas the prosobranch studied only removed overlying filamentous algae (Barnese *et al.*, 1990). The argument that the type and amount of food resources available determine gastropod distributions implicitly assumes that resources are limiting and intra- and interspecific competition are, therefore, more likely. Considerable debate has occurred on the role of competition in structuring communities (Strong *et al.*, 1984), but two literature reviews found substantial empirical evidence for competition (Connell, 1983; Schoener, 1983). Likewise, a recent statistical meta-analysis combining a large number of empirical studies (Gurevitch *et al.*, 1992) supported a role for competition, even in herbivores, contrary to the Hairston-Smith-Slobodkin hypothesis (Hairston *et al.*, 1960).

Several direct or indirect observations suggest that competition could occur among snails: (1) dense gastropod assemblages do limit their food resources (Sheldon, 1987; Osenberg, 1989; Bronmark *et al.*, 1992; Hill *et al.*, 1992; Rosemond *et al.*, 1993); (2) species diversity increases with increasing habitat complexity (Harman, 1972; Brown and Lodge, 1993); and (3) field sampling surveys suggest that fewer congeners coexist than expected by chance (Harman, 1968; Harman and Berg, 1971; Dillon, 1981, 1987). Brown (1982) experimentally demonstrated competition between two vernal pond snails. These populations

occurred in ephemeral ponds, but because significant niche overlap occurred in only one of six possible pair-wise combinations of species, interspecific competition was probably not a structuring force in these fluctuating lentic habitats. However, in more permanent habitats like lakes or large rivers that have more diverse assemblages, competition might be more likely. For example, up to 14 gastropods are often found in macrophyte beds in lakes in northern Wisconsin (Brown and Lodge, 1993).

In Table 1, we list four specific hypotheses about important regulating factors, and our prediction in each case of the relative abilities of pulmonates and prosobranchs in coping with the factor, based on the existing knowledge of gastropod ecology outlined above. It is our hope that these hypotheses will form the basis for understanding the distri-

Table 1. Specific hypotheses and predictions on ecological differences between pulmonates and prosobranchs, and how these differences can affect distribution patterns.

Hypothesis 1: Relative competitive abilities are important in determining lotic gastropod distributions.

    Predictions

        P_1 - Pulmonates, with finer radular teeth, are better at removing adnate algae, giving them a competitive advantage when food is a limiting factor.

        P_2 - *Elimia* and other prosobranchs are poorer competitors if food is a limiting factor.

Hypothesis 2: Disturbance events like spates and the relative dispersal/colonization abilities of gastropods are important factors affecting snail distributions.

    Predictions

        P_1 - Pulmonates are better dispersers (*e. g.* greater passive dispersal by birds and greater locomotory rates) and are suited to headwaters with high frequencies of spates.

        P_2 - Prosobranchs (with the possible exception of *Elimia*) are poorer dispersers and less resilient to spates.

Hypothesis 3: Physiological adaptations are important in determining gastropod distributions.

    Predictions

        P_1 - Pulmonates are most tolerant to extreme physical and chemical variables (*e. g.* temperature, hypoxia, and dessication) making them better adapted to temporary headwaters and shallow littoral areas.

        P_2 - *Elimia* and other prosobranchs are less tolerant to extreme temperature and hypoxia but survive as well in middle reaches where flow is sustained.

Hypothesis 4: Predation pressure increases with river order and is a significant factor determining snail distributions.

    Predictions

        P_1 - Pulmonates are most susceptible to predation because of their thin shells, and are restricted to headwaters or shallow littoral zones where fewer predators occur.

        P_2 - Prosobranchs are less susceptible to predation and can co-occur with abundant and diverse predator assemblages (both fish and crayfish) of larger streams.

butional ecology of gastropod assemblages, especially those that contain threatened or endangered species.

We also present data that bear on at least some of these hypotheses. Specifically, we sampled one river system, the Salt River in western Kentucky, to determine if there were any longitudinal differences in the distributions of pulmonates and prosobranchs. To gauge differences in in-stream dispersal among several pulmonate and prosobranch species, we measured locomotory rates and righting responses in laboratory experiments. Crawling rates are obviously related to dispersal within streams; we consider righting responses to be important as well because detached snails would be more susceptible to being washed downstream. An artificial stream was used to conduct a month-long competition experiment between one pulmonate common in headwaters of the Salt River and one prosobranch common in the Ohio River. We evaluated data in the literature on the physiological adaptation of both groups to temperature and dissolved oxygen extremes. Finally, we discuss existing work on differential predation risk of pulmonates and prosobranchs (done mostly with lentic species) and present some data on relative vulnerability to crayfish of a head-water pulmonate found in the Salt River and a prosobranch species common throughout much of the river system.

METHODS

Habitat description and sampling methods

The Salt River is a tributary system of the Ohio River located east and south of Louisville, Kentucky, with an average annual discharge of 51 m³/sec (based on 6 years of data, United States Geological Survey, Kentucky Water Division). The headwaters of the river originate on the flat, forested lands east of Louisville in small marsh-like springs, and these headwaters often dry late in the hydrological cycle in summer and fall. The higher order creeks in the system are often deeply incised into the karst topography of the area, with very little littoral zone habitat. The Salt River watershed includes large tracts of relatively undisturbed eastern deciduous forest, but some branches of the river drain agricultural and suburban areas near Louisville. The riparian zone is typical of lowland, eastern deciduous forest streams (but also includes some disturbed, open canopy areas), and substrata vary from limestone cobble in headwaters to a clay/silt bottom in downstream reaches.

We collected data on relative gastropod abundance in both fall 1994 and spring 1995 from headwaters to large-order sites of the Salt River. Our approach was to sample vegetation, leaf debris, and erosional limestone habitats using kick-nets and visual searching (*e. g.* turning over

rocks, leaves, and snags) for at least 30 min at each site, or until continued sampling suggested no additional changes in the relative abundance of snail species. We explicitly avoided collection sites near urban or agricultural influences, to minimize problems with human alterations of the streams. All snails collected were fixed in 70% ethyl alcohol and were later identified using keys by Burch (1982), Branson (1987), and Brown (1991). We noted the number of sites, in several categories of river orders, in which each species was found, as well as the total number of individuals collected. We used a G-test of independence to determine if the relative abundance of prosobranchs was independent of river order.

Relative dispersal abilities

To be conservative, we considered only differences in in-stream dispersal ability between the two groups. In a series of laboratory experiments (winter to spring 1995), we measured differences in two behaviors that should be related to in-stream dispersal ability: turnover times (e. g. righting responses) and rates of movement. To measure the first variable, we recorded the time necessary for individuals to right themselves after being detached from the substratum (N = 17-38 individuals, depending on species). Solitary animals were placed in Syracuse dishes (5 cm high x 10 cm diameter) in 200 ml of standard reconstituted freshwater (hard water type; APHA, 1985) at room temperature (22-26°C). The four species with spiral shells (*Physella, Elimia, Pleurocera*, and *Lithasia*) were turned over onto the dorsal sides of their shells. Because of its sinistral, planospiral shell, *Helisoma* was turned over on its right side. Each snail was lightly prodded (with a blunt probe) to withdraw into its shell, or to release any air in the pulmonate mantle cavities which would cause the snail to float. The time necessary to extend the foot and reattach to the substratum was recorded.

Movement rates were recorded (N = 31-42 individuals, depending on species) by placing solitary animals in clear plastic chambers (26 x 16 x 10 cm high) in 800 ml of standard reconstituted freshwater at room temperature. After allowing 300 s for habituation, the snail's movement rate across the container was recorded on a 2 cm gridded surface for 300 s. In both cases, we contrasted differences among species with a one-way analysis of variance.

Competition experiment

To gather evidence on competitive abilities, we performed a month-long (September 1994) experiment in artificial stream mesocosms at Louisville Water Company's Payne water treatment facility. The artificial streams received filtered (large debris removed) water and sediment from the Ohio River. The stream channels were shaded, rectangular polyvinyl chloride troughs (10 cm depth and width x 3 m length). Water level (1 cm at the inflow, 7 cm at the outflow) was maintained by a computerized pump system attached to a header tank. Outflows were covered with 1 mm mesh weirs to contain the snails. Streams were not stocked with artificial substrata or periphyton, but they did develop a silt substratum ranging from 1 to 3 cm with rich coverings of filamentous green algae.

We selected two species from separate ends of our river gradient, *Helisoma trivolvis* (a pulmonate found in headwater streams, see Results) and *Lithasia obovata* (Say, 1829) (a large river prosobranch) and maintained them alone and in mixed populations in an additive design (Snaydon, 1991). Densities of 30 individuals per species per channel were chosen to be representative of field densities, based on sampling data (K. Greenwood, University of Louisville, unpubl. data), and six replicates were completed in each of the three (two mono-specific and one mixed) treatments. Each mono-specific treatment used 30 snails, and the mixed treatments used 30 of each species. Although total snail biomass does vary among treatments in such an additive design (versus the substitutive design with total numbers held constant in all treatments), additive designs are considered superior because they do not confound the effects of intraspecific and interspecific competition (see detailed arguments by Snaydon, 1991). By comparing the reduction in growth of each species under mixed conditions, relative to each other, one can still judge relative competitive abilities. We also selected these two species because they are of roughly the same individual biomass, with *Lithasia* slightly larger (mean wet mass = 305 mg ± 20 mg SE) than *Helisoma* (217 ± 20 mg). Each snail was weighed (± 1 mg) before and after the experiment to determine the impacts on growth (increase in mean individual biomass per stream channel). To test for differences in growth, we performed a two-way analysis of variance (two species times alone versus mixed) on per capita growth rate, using the stream channel as the experimental unit.

Predation experiment

Little is known about the relative vulnerabilities of gastropods to invertebrate predators. Because of this, we performed laboratory experiments on selectivity of the crayfish *Orconectes virilis* (Hagen, 1817), which is quite abundant in the Salt River drainage. Overnight trapping in early October 1994 suggested high abundance (mean individuals/trap = 26.4 ± 5.7 SE, N = 8) in Guist Creek, a fourth-order tributary of the Salt River located 50 km east of Louisville. These trapping rates were greater than those in Wisconsin lakes where crayfish predation was experimentally shown to control snails (Lodge *et al.*, 1994). Trapping rates could have been high because October is the low point in the river drainage's hydrological cycle. Guist

Creek was essentially a series of disconnected pools, further concentrating the crayfish.

Crayfish were held overnight in 40 l aquaria with brick refuges before being used in experiments. Our experiments used methods developed by Alexander and Covich (1991a, b) and Covich *et al.* (1994). A single, male crayfish (mean carapace length = 40.8 mm ± 0.7 mm SE) was held in a 2 l aquarium overnight with 25 each of adult *Physella heterostropha* (Say, 1817) and *Elimia semicarinata* (Say, 1829). Experiments were completed at room temperature with 1 l of EPA reconstituted water. Numbers of snails escaping vertically above the water line were observed next morning, to determine the fraction of surviving snails actually available to the crayfish. We tested for a difference in crayfish preference for the two species with a paired t-test (Peterson and Renaud, 1989).

RESULTS

Sampling survey

A clear pattern emerged (Table 2) with pulmonates (*Physella heterostropha, Helisoma trivolvis*) found mostly in first- or second-order streams. Physids were found at nine of the 12 sites, and *Helisoma* was found at five of the 12 sites in streams of first or second order, indicating that they were fairly widespread in temporary headwater streams. The prosobranch *Elimia semicarinata*, also common in headwaters, was the numerical dominant in third to fifth order streams: physids were found at three of the 11 sites, *Elimina* at ten of the sites, and *Pleurocera acuta* Rafinesque, 1831, at five of the sites. Along with *Elimia*, pleurocerids *Lithasia obovata* and *P. acuta* were also found in rivers of orders 6 to 9. Finally, at several littoral sites along the Ohio River, *P. canaliculata* (Say, 1821) and *L. obovata* were the dominant gastropods. Thin-shelled species such as *Physella* are extremely rare in littoral zone habitats of the Ohio River, based on our experience (J. Alexander, pers. obs.). A G-test of independence (Sokal and Rohlf, 1981) contrasting pulmonate and prosobranch distributions across the river orders was highly significant ($G = 707$, $P < 0.001$), indicating that the two groups were not distributed in the same fashion across river size categories. Based on studies of nearby streams (Branson and Batch, 1983; Johnson *et al.*, 1994), we believe that the trend (*e. g.* replacement of pulmonates by prosobranchs) is common.

Relative dispersal abilities

An Analysis of Covariance indicated that there were significant differences among species in righting response (species effect $F_{4,139} = 40.9$, $P < 0.0001$), but that size (the covariate) did not have a significant effect (covariate $F_{1,139} = 3.3$, $P = 0.07$). Tukey's *a posteriori* ranges (Fig. 1) indicated that *Physella* had a significantly faster righting response than all other species, and that *Lithasia* was significantly slower than all other species except *Pleurocera*.

Physella heterostropha also crawled at a rate four times faster than the other four species (species $F_{4,139} = 38.8$, $P < 0.0001$), with shell length again having little effect (covariate $F_{1,139} = 0.4$, $P = 0.53$). Tukey's *a posteriori* ranges suggested that the other four gastropods had similar crawling rates (Fig. 1).

Competition experiment

Although *Helisoma* and *Lithasia* grew at different rates in monocultures (species $F_{1,22} = 19.8$, $P < 0.001$; Fig. 2), significant evidence of interspecific effects on growth was present for each species as well (alone versus mixed $F_{1,22} = 40.6$, $P < 0.001$). The competitive effect was quite asymmetrical (*i. e.* interaction $F_{1,22} = 20.6$, $P < 0.001$), with the pulmonate suffering a 92% reduction in growth, versus 55% in the prosobranch.

Predation experiment

The crayfish in the current study strongly preferred *Physella* over *Elimia* (means of 50% consumed versus only 0.7 % of the prosobranchs; N = 11, paired t-test, P < 0.001). Almost two-fifths of the remaining physids had crawled out, and none of the prosobranchs, indicating that predation is still differential, even when vertical escape is possible for the thinner-shelled physid (see also Alexander and Covich,
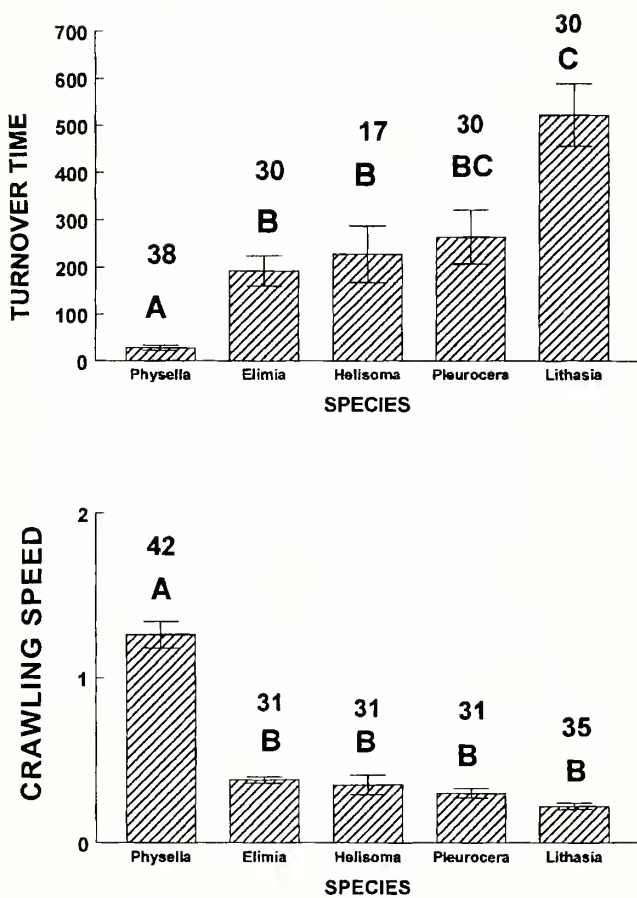
Table 2. Numbers of gastropods collected in the Salt River, Kentucky, according to river order of each site. The number of sites (N) where each gastropod was collected are indicated in parentheses.

Species	River Order			
	1 - 2	3 - 5	6 - 9	10 or above
	(12)	(11)	(2)	(3)
Physella heterostropha	219 (9)	13 (3)	0	0
Helisoma trivolvis	42 (5)	0	0	0
Elimia semicarinata	726 (5)	1764 (10)	149 (1)	0
Pleurocera acuta	0	17 (5)	166 (2)	0
Lithasia obovata	0	0	710 (1)	143 (2)
Pleurocera canaliculata	0	0	0	72 (2)

Fig. 1. Comparison of turnover time (righting response time) in seconds (top, mean ± SE, N above histogram) and average crawling speed in millimeters per second (bottom, mean ± SE, N above histogram) for two pulmonates (*Physella* and *Helisoma*) and three prosobranch snails. Means with different letters are significantly different (P < 0.05), based on Tukey's *a posteriori* ranges.

1991a, b).

DISCUSSION

Differences in physiological adaptations

A considerable amount of work has been done on the physiological ecology of freshwater snail species, although few comparative studies of lotic species have been undertaken. We therefore summarize the arguments and data presented in reviews of pulmonates (McMahon, 1983) and prosobranchs (Aldridge, 1983). Both authors maintained that pulmonates, which were typically found in shallow, physically and chemically more-variable environments, had broader tolerance adaptations to temperature. However, the ranges reported in field studies were fairly similar (mean range ± SE for pulmonates of 28.2 ± 1.4°C, N = 12 populations, versus a mean range of 26°C for the two prosobranch studies). The mean upper temperature reported for the pulmonates was 30.9°C versus 27°C for the

prosobranchs (data presented by McMahon, 1983). However, although the two thermal maxima were similar, pulmonates have been reported in earlier studies to have some of the highest thermal maxima in multicellular animals (Van der Schalie and Berry, 1973; Russell-Hunter, 1978; McMahon, 1983, 1985). For example, physid species are capable of activity under ice cover, and have also been reported in warm springs.

Pulmonates clearly show greater capacity adaptations to changing temperatures. Laboratory studies have suggested that the metabolic rates of pulmonates change less with increasing temperature than those of prosobranchs. The experimental studies, summarized in Table 3, indicate significantly lower Q_{10} values for metabolic rates across the same temperature range (t = 2.1, 0.02 < P < 0.05, DF = 28). With Q_{10} values nearer 2.0 (measured in their ambient temperature range), pulmonates can better regulate acute temperature change effects on their metabolic rates (McMahon, 1983). Six of ten pulmonates, versus zero of seven prosobranchs, had Q_{10} values below 2.0. This ability
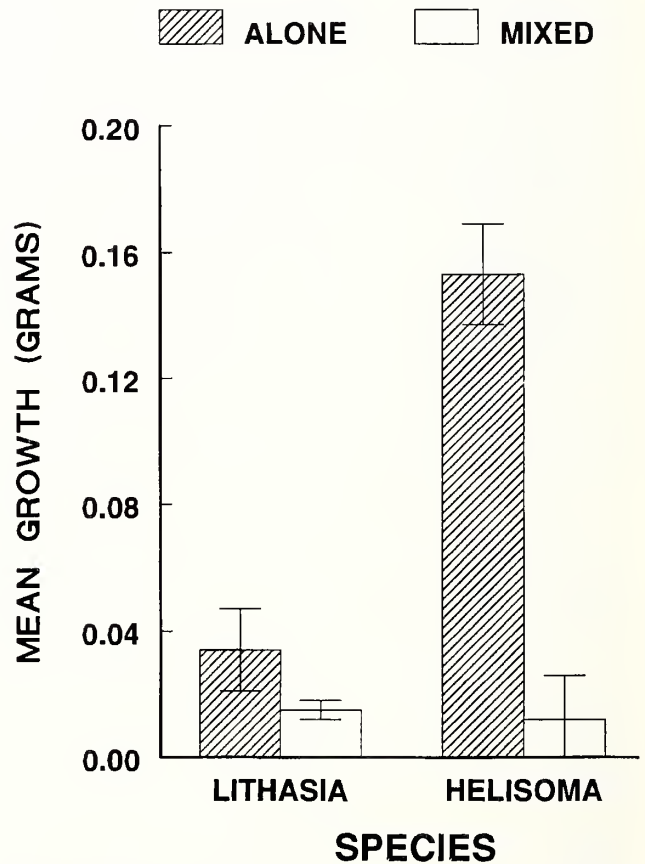

Fig. 2. Results of a month-long competition experiment in artificial streams where each species was reared alone and compared to a mixed population in an additive design. Data are mean increases in individual biomass per stream ± SE, N = 6.

to regulate metabolic rate during acute temperature changes may be an adaptation to life in fluctuating, shallow-water habitats. Prosobranchs may not need metabolic regulation, because they are common in deeper, more permanent, and more thermally stable habitats (McMahon, 1983). McMahon (1983) also pointed out that most pulmonates can reproduce across a broader temperature range than can prosobranchs, again a valuable adaptation in variable aquatic habitats.

Differences between pulmonates and prosobranchs in resistance and capacity adaptations to hypoxia are more complicated. In regard to tolerance, Aldridge (1983) noted that prosobranchs require higher oxygen levels in water than do pulmonates (Boycott, 1936; Palmieri *et al.*, 1980), but this could simply be because pulmonates can use pulmonary (*i. e.* aerial) respiration. Prosobranchs are more resistant to hypoxia in laboratory experiments when aerial respiration is not possible (Von Brand *et al.*, 1950; Hawkins and Ultsch, 1979). There is also variation in resistance to hypoxia within pulmonates. For example, planorbids with their respiratory pigments are more tolerant (and more aquatic) than lymnaeids and physids; the latter two groups rely more on pulmonary respiration and are more amphibious (McMahon, 1983; Alexander and Covich, 1991b; Covich *et al.*, 1994).

Pulmonates clearly have greater capacity adaptations to variation in oxygen concentration, although some background on experimental methods is necessary to illustrate this. In Table 3, the degree of metabolic regulation in response to declining oxygen levels is compared between the two groups by fitting standardized metabolic rate versus PO_2 (partial pressure of oxygen in water) in a quadratic equation (Mangum and van Winkle, 1973), with standardized uptake = $a + b_1(PO_2) + b_2(PO_2)^2$. The quadratic coefficient (b_2, multiplied by 10^3) is the dependent variable, and the degree of metabolic regulation is determined using statistical methods (Mangum and van Winkle, 1973; McMahon, 1985). Values of b_2 (10^3) near -0.1 indicate nearly perfect regulation (the metabolic rate under hypoxia is very near that at air saturation), whereas values near zero indicate conformity, where metabolic rates are a linear function of oxygen concentration (Mangum and van

Winkle, 1973). Pulmonates do possess values of b_2 significantly less than those shown by the prosobranchs (t = -3.15, P < 0.01, DF = 17). This result is somewhat surprising (because pulmonates are evidently more sensitive to sustained hypoxia); however this could again reflect their common occurrence in shallow-water environments that are frequently exposed to diurnal cycles of hypoxia.

In summary, pulmonates evidently have smaller tolerance adaptations to long-term hypoxia (they could be able to avoid this problem with aerial respiration) but greater capacity adaptations. Pulmonates are also better adapted to resist desiccation because they can use pulmonary respiration, store their nitrogen excretory products as urea (not ammonia), and can aestivate by forming an epiphragm covering their aperture (McMahon, 1983; Brown, 1991) to minimize water loss.

The fact that pulmonates show smaller changes in metabolic rates to changing temperature or oxygen tension could be critically important in an ecological sense. Gastropods with lower maintenance costs under extreme physical or chemical conditions would have more energy to partition into growth or reproduction, and thus show greater fitness and/or competitive ability. Differences between pulmonates and prosobranchs in shell thickness and reliance on aerial refugia (and aerial respiration) could be contrasting adaptations due at least in part to different life histories and evolutionary pathways in the two groups (Vermeij and Covich, 1978; Alexander and Covich, 1991a, b; Covich *et al.*, 1994).

Literature studies of predation

In Table 4, we have summarized earlier studies of selectivity of fish and crayfish molluscivores in lentic and lotic systems. In the two studies of molluscivorous sunfish (Stein *et al.*, 1984; Klosiewski, 1991), there was a clear preference for thin-shelled pulmonates like *Physella* or *Helisoma* over prosobranchs like *Elimia* or *Campeloma*. Experimental results on selectivity of orconectid crayfish in Wisconsin lakes (Brown, in press) also indicated thin-shelled species like *Physella* and *Gyraulus* are consumed

Table 3. Differences in regulation of metabolic rates as a function of temperature (Q_{10}) and as a function of partial pressure of oxygen (b_2) between pulmonate and prosobranch snails. Data from McMahon (1983). See text for statistical tests of the differences between the two groups.

Group	Mean Q_{10} + SE (N)	b_2 (x 10^3) + SE (N)
Pulmonates	2.12 ± 0.09 (18)	-0.061 ± 0.009 (12)
Prosobranchs	2.76 ± 0.29 (13)	-0.014 ± 0.012 (7)

Table 4. Summary of earlier studies of selectivity among molluscivores.

Predator	Habitat	Preference	Reference
Red-ear sunfish	Ohio rivers	*Physella* > *Helisoma* > *Elimia*	Stein *et al.*, 1984
Pumpkinseed sunfish	Wisconsin lakes	*Lymnaea* > *Amnicola* > *Campeloma*	Klosiewski, 1991
Orconectes spp.	Wisconsin lakes	*Gyraulus* > *Physella* > *Amnicola*	Brown, in press

more frequently than *Amnicola* spp.

Evaluation of hypotheses regarding pulmonates and prosobranchs

The results of sampling the Salt River support our predictions of where pulmonates and prosobranchs should occur. Specifically, the lack of thin-shelled species like *Physella* in large rivers could be due to a greater diversity, abundance, or greater body size of fish predators, whereas thick-shelled species (*e. g. Pleurocera canaliculata*) could be absent from from the more temporary headwater streams due to desiccation or hypoxia resulting from low or intermittent flow, or because of relatively poor dispersal abilities. Pulmonates might also be feeding generalists or have more success at repopulating disturbed sites because of their "r-selected" life histories. Although pulmonates as a group are considered micro-herbivores, *Physella* and *Helisoma* are feeding generalists (Brown, 1982, 1991).

Some aspects of these distribution patterns, however, could be unique to the Salt River system. Little shallow-water macrophyte habitat occurs along the Salt River because of the constrained nature of the littoral zone, a function of the river eroding a steep channel in the limestone substratum. In river systems with extensive marsh-like littoral zones, pulmonates could be more common along the edges of rivers. However, we do not consider this type of horizontal distribution pattern in rivers as repudiating our general hypothesis. These littoral macrophytes might provide shelter from predators, and shallow littoral habitats are again expected to vary more in physicochemical variables than the main river channel. Similarly, many southeastern U. S. rivers originate from springs, or have montane headwater reaches that are quite turbulent. In these systems we might actually expect a preponderance of prosobranchs in headwaters, because turbulence increases dissolved oxygen levels, or because spring sources vary little in physicochemical variables (see data in Johnson *et al.*, 1994). Pulmonate species might become more common downstream, because of the addition of more ephemeral littoral zone habitats, or greater variation in physicochemical variables (P. Johnson, Southeastern Aquatic Research Center, unpubl. data.; Foin and Stiven, 1970; Dillon and Benfield, 1982). Again, such distributional patterns would not contradict our general hypothesis. Finally, the prosobranch *Elimia* was common in both the headwaters and middle reaches of the Salt River, contrary to our prediction that pulmonates should dominate headwaters. Perhaps those particular headwaters are less susceptible to drying.

The experimental results and literature review also suggest support for some of our hypotheses. An exception is that the prosobranch, *Lithasia*, a common denizen of higher-order rivers, appeared to be a better competitor than the headwater pulmonate, *Helisoma*. Growth declined less under interspecific competition in this large-river prosobranch than in the pulmonate. The result is again somewhat surprising in light of earlier research suggesting that pulmonates, as a group, crop periphyton resources more closely to the substratum (Barnese *et al.*, 1990). However, the earlier study was completed in a lentic habitat, and only one species of prosobranch, *Elimia livescens* (Menke, 1830), was compared to several pulmonates. Also, there is considerable variation *within* pulmonates in grazing ability. For example, lymnaeids are, because of differences in radular anatomy, better adapted to removing filamentous algae than are physids, whose complex teeth are better at removing adnate diatoms (see references by Brown, 1991). Thus, differences in grazing ability could depend on the particular pulmonate or prosobranch family in question.

Because *Lithasia* is most common on littoral-zone cobble along the Ohio River, we would not have a *priori* predicted it would do better than the pulmonate, which occurs in soft sediments such as those lining the bottom of the experimental channels. We would have also expected that the relatively short time-span of the experiment would have favored the pulmonate, because of its short life cycle. However, it is also important to note that *Lithasia* and *Helisoma* do not overlap in nature, being at opposite ends of the river continuum, and thus lack an extensive history of competition.

The evidence for dispersal ability as a limiting factor in field distributions is equivocal. *Physella* clearly is the most active species and disperses at a higher rate, as expected because it is most common in headwater environments. However, *Helisoma*, which is also common in the same environments, moves no faster than any of the prosobranch species, including *Lithasia* and *Pleurocera*, which are found only in medium to large rivers. Of course, both pulmonates could have greater passive dispersal abilities, as mentioned earlier, a factor which we did not investigate, and pulmonates can also self-fertilize, a valuable aid in colonizing new habitats.

The available data in the literature do seem as a whole to indicate that pulmonates are better adapted physiologically to the large range of physical and chemical variation occurring in ephemeral habitats like shallow littoral zones, or the seasonal headwater habitats in the Salt River. Conventional wisdom is that pulmonates show broader resistance and capacity adaptations to temperature. The capacity adaptations of pulmonates to variation in dissolved oxygen are at least as great as in prosobranchs, and pulmonates can respire aerial oxygen. Pulmonates are also better at resisting desiccation. In addition, prosobranchs do not have the ability to aestivate and survive over periods when habitats dry.

Finally, both our experimental results and the literature clearly suggest the importance of predation as an eco-

logical factor determining lotic gastropod distributions. As stream order increases, it is likely that the abundance of crayfish (and probably other invertebrate predators) at first increases, and then decreases as fish become more abundant and diverse (Crowl, 1990). The thick shells of prosobranchs afford them better protection from fish (Stein *et al.*, 1984; Klosiewski, 1991) and crayfish predation (this study). They also have an advantage against other shell-invading invertebrate predators like leeches because they possess an operculum (Bronmark and Malmqvist, 1986; Brown and Strouse, 1988).

Suggestions for future research

This paper clearly demonstrates the need for further work on the community ecology of lotic gastropods. It has been our purpose to establish several hypotheses (that are not necessarily mutually exclusive) explaining gastropod distributions along river continua, rather than to definitively identify which hypotheses are most important. For example, future studies could examine the competitive ability of all species in the replacement series in a particular river system to determine, for example, if the competitive hierarchy is transitive. These studies should also gauge the relative importance of intraspecific competition (*e. g.* density dependence) and interspecific competition for both snail groups. Although such a comparative study might prove difficult, future researchers could also test the differential passive dispersal hypothesis by sampling birds and other vertebrates arriving at lotic sites to determine the relative abundance of phoretic juvenile gastropods. Future physiological research should test for differences in capacity and tolerance adaptations among co-occurring sets of gastropods found along river continua to rigorously test the conventional wisdom that pulmonates are better adapted to physically more extreme habitats. Also, although comparative work has been done on pulmonates, very little is known of differences in physiological tolerances among prosobranchs. In addition, little is known of the comparative tolerances of pulmonates and prosobranchs to other potentially important physiological stresses occurring at different points along the river continuum, such as spates, turbidity, and wave action.

We hope that this paper will stimulate future research in understanding the community ecology of riverine snail assemblages, and thus help preserve the rich gastropod assemblages found in many southeastern U. S. river systems. This is especially important because as many as one-third of the species face threats of extinction (Neves *et al.*, 1998). Although they are relatively unstudied, prosobranch gastropods like *Elimia* are important as grazers in southeastern U. S. lotic systems (Richardson *et al.*, 1988; Hill *et al.*, 1992; Rosemond *et al.*, 1993). A vital first goal for conservation efforts is to more fully understand what

ecological and evolutionary factors constrain the ranges and population biology of these lotic gastropods.

ACKNOWLEDGEMENTS

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